For example, if $r = 1.5$ (so that the nuclear volume of any cell increases 50 per cent. when that cell divides), then for the result of four cleavages (producing 16 cells) the formula gives

$$x = \frac{(1.5)^3 - 1}{2^4 - 2} = \frac{2.375}{14} = 16.96 \text{ per cent.}$$

If Conklin employed the 1-cell stage as his standard of comparison, the above formula would be

$$x = \frac{r^n - 1}{2^n - 1}. \tag{2}$$

It will be found that for any increase less than 100 per cent. of what was present before division (that is, $r = 2$), Conklin's ratio (from formula 1 or 2) decreases in the later stages of cleavage, even though the law of increase, so far as each cell by itself is concerned, remains absolutely the same. Thus, if at the division of every cell its nuclear volume increases 50 per cent., Conklin's ratio (formula 1) will give 25 per cent. for the result of the second cleavage, 20.83 for the third, 16.96 for the fourth, 13.54 for the fifth, 10.64 for the sixth, 8.25 per cent. for the seventh, etc. This appears to be the reason why Conklin finds the rate of nuclear increase, as shown by his ratio, to be less in later stages; it is not due to any change in the relations so far as what happens in each cell is concerned.

H. S. JENNINGS

IS THERE ASSOCIATION BETWEEN THE YELLOW AND AGOUTI FACTORS IN MICE?

IN the generally accepted formulæ for the colors of mice, as worked out by Cuénot, Bateson, Durham and others, there is assumed to be a factor, Y, for self yellow color,[1] which is epistatic to T, the ticking or agouti factor (also known as G). The various types have the following constitution:

Yellow	$Yt\ yt$, or $Yt\ yT$.[2]
Agouti (including cinnamon)	$yT\ yT$, or $yT\ yt$.
Black and chocolate (including dilute forms)	$yt\ yt$.[3]

[1] On the formulæ adopted here this factor Y is probably to be considered an inhibitor.

[2] It has been shown by Cuénot and others (see especially Castle and Little, *Science*, N. S., 32, 868, 1910) that mice homozygous for Y do not exist, the reason probably being that the YY zygotes, though formed in the expected proportions, do not develop.

[3] Blacks differ from chocolates in having a black factor, B. Agoutis also carry this factor, while cinnamons lack it. Yellows may or may not bear it, but the two types are distinguishable by their eye color.

If yellow mice of the sort one usually obtains be bred together they produce yellows, blacks and chocolates—almost never any agoutis. But if such yellows be bred to agoutis and their yellow offspring be mated together the result is only yellows and agoutis. It has been pointed out by Morgan[4] that this last result is inconsistent on the current formulæ, since blacks or chocolates should also be expected. For example, if we assume, as I think we must, that ordinary yellow mice usually have the constitution *Yt yt,* then the cross under discussion would be as follows:

Yellow—*Yt yt*
Agouti—*yT yT*

Yt yT—yellow
yt yT—agouti
F_1 yellow—gametes—*YT Yt yT yt*

F_2

YT *YT*	*YT* *Yt*	*YT* *yT*	*YT* *yt*
Yt *YT*	*Yt* *Yt*	*Yt* *yT*	*Yt* *yt*
yT *YT*	*yT* *Yt*	*yT* *yT*	*yT* *yt*
yt *YT*	*yt* *Yt*	*yt* *yT*	*yt* *yt*

Total, omitting all *YY*'s: 8 yellows, 3 agoutis, 1 black or chocolate.

It seems to me that the easiest way of explaining why this mating actually does not produce blacks and chocolates is by the assumption of linkage or association ("gametic coupling") between the agouti and yellow factors. The fanciers, from whom most yellows come, ordinarily keep few agouti mice. It is therefore probable that most yellows carry no *T,* and for this reason *Y* and *T* really show "spurious allelomorphism" or repulsion instead of "gametic coupling."[5] There seems to be no evidence that *Y* and *T* ever occur in the same gamete. The evidence which has led to this conclusion is as follows:

Miss Durham[6] has found that if ordinary yellows be mated

[4] *Ann. N. Y. Acad. Sci.,* 21, 87, 1911. It was at Professor Morgan's suggestion that I took up this problem.

[5] I shall use the term association to cover both coupling and repulsion.

[6] *Journ. Genet.,* 1, 159, 1911.

together they produce two yellows to one black or chocolate, no T being present. Her total figures are 451 yellows to 241 blacks and chocolates, to which should be added Little's[7] record of 31 yellows to 24 blacks and chocolates. If ordinary yellows be mated to chocolates or blacks the result is an equal number of yellows and of blacks or chocolates. Miss Durham's figures are 282 yellows and 319 blacks and chocolates. Both these crosses are cases of monohybridism, T never being present, and Y alone being involved.

If ordinary yellows be bred to pure agoutis, the result should be equal numbers of yellows and agoutis, as shown above. The actual results obtained are as follows:

Yellow	Agouti	Authority
53	39	Durham.
16	14	Morgan.
69	53	

If the P_1 agouti used in this cross were heterozygous in T, then the expectation would be two yellows, one agouti, and one black (or chocolate). Apparently Morgan is the only one who has reported such a cross. He obtained 4 yellows, 5 agoutis, and 1 black.

The results of the four crosses above are explicable without the assumption of association between T and Y, since in no case was an animal bred from which was heterozygous in both, and only in such cases does association ever become apparent. But such heterozygous mice should be obtained in the cross between agouti and yellow. If these be mated together the ordinary expectation, as shown by the diagram above, would be 8 yellows, 3 agoutis, and 1 black or chocolate. The actual offspring recorded from yellow by yellow giving agouti are:

Yellow	Agouti	Black and Chocolate	Authority
108	62	0	Durham.
15	9	0	Morgan.
123	71	0	

This is approximately two yellows to one agouti. It is the result which would be expected if one of the parent yellows were pure for T (TY Ty). But, with the possible exception of 20 of Miss Durham's,[8] all the above 194 mice were from yellows out of yel-

[7] *Science*, N. S., 33, 896, 1911.

[8] It would appear from the context that these 20 also belong to the category under discussion, but a definite statement to that effect is not given.

low by agouti. No other crosses of yellow by yellow gave agouti, so that it seems in the highest degree probable that the original (P_1) yellows were pure for t. That being the case the F_1 yellows must all have had the formula $tY\ Ty$. But since they produced only ⅔ yellows to ⅓ agoutis it follows that association occurs between T and Y, thus:

$$\begin{array}{ll}
\text{Yellow—}tY\ Ty & \\
\text{Yellow—}tY\ Ty & \\
\hline
\quad Ty\ tY & \\
\quad tY\ Ty & \text{—2 yellows.} \\
\quad (tY\ tY) & \\
\quad Ty\ Ty & \text{—1 agouti.}
\end{array}$$

These T-bearing yellows have also been bred to chocolates and blacks. If there were no association this mating should produce two yellows, one agouti, and one chocolate or black. But Miss Durham has obtained only 30 yellows and 37 agoutis—practically equal numbers, with no blacks or chocolates. On the association hypothesis this cross should produce the following result:

$$\begin{array}{rl}
\text{Yellow—}tY\ Ty & \\
\text{Chocolate or black—}ty\ ty & \\
\hline
tY\ ty & \text{—1 yellow.} \\
Ty\ ty & \text{—1 agouti.}
\end{array}$$

Apparently the ticking factor and the factor which produces yellow mice are associated very closely. There appears to be no evidence that "crossing over" ever occurs. It can not be supposed that Y is the same as t, with which it always occurs, since in that case all mice not agouti, or even heterozygous for T, would be yellow, and black and chocolate would not exist. It should be noted that if one adopts Castle's mouse formulæ (see Castle and Little,[9] etc.), it is still necessary to suppose that association occurs but now between the restriction factor, R, and the agouti factor, A.

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February, 1912

[9] *Science*, N. S., 30, 313, 1909.